

Effects of Tillage on Invertebrates in Soil Ecosystems

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10.1 INTRODUCTION

Soil serves as a permanent or temporary habitat for several faunal groups. Animals of different shapes, body sizes, and taxonomic classes dwell in both natural and human-managed agricultural soils. Terrestrial invertebrates are highly adapted to these living conditions. Inhabitants of the soil surface and topsoil rely on both food

and shelter in these environments. Body pigmentation, higher mobility, and a higher resistance to weather extremes distinguish epigeal arthropods (see [Chapter 11](#)) from the true inhabitants of deeper soil layers. In contrast to the surface fauna, there are other soil inhabitants that can build and shape their own living sites. In burrows, forming tubes, and stabilizing cavities, earthworms and enchytraeids are good examples of soil-building and soil-forming edaphic groups as they burrow channels, form tubes, and stabilize cavities. The contribution of these worms is not limited to soil-building processes alone but in addition to many other functions ([Chapter 9](#)) including the formation of the living sites for several soil animal groups. Unlike epigeal and burrowing species, true soil inhabitants—mostly belonging to the meso- and microfauna¹—are entirely dependent on “prepared” pores, tubes, cracks, or channels as habitats. Highly diverse communities, including Protozoa, Nematoda, Myriapoda, Acarina, Insecta, and Oligochaeta, colonize air-filled spaces, aggregates, or water-filled pores. Together with bacteria, fungi, actinomycetes, and algae they build up the large bulk of soil biota, also known as the Edaphon. Water films coating soil mineral particles and water-filled pores are centers of decomposition activity, driven mainly by microorganisms. The significance of bacteria, fungi, Protozoa, and nematodes for soil biological activity has been repeatedly emphasized⁶⁸ in other chapters of this book, and particular attention was given to microbial organisms in [Chapter 3](#).

The importance of the soil biota in agroecosystems lies not only in their significant role in soil-building processes (pedogenesis)² but also in their vital functions in soil food webs. Changes to any of these functions would result in disturbance of the ecosystem involved.^{3,4} Rearrangements of the soil profile caused by tillage are considered as dramatic interventions with far-reaching implications for the edaphon, nutrient cycles, and ecosystem stability. Nonburrowing species with low potential for population recovery may suffer most from the effects of tillage. Hence, shifts in community structure and species dominance in addition to changing soil environments are likely to disrupt existing relationships among organisms. The affected interactions between different trophic levels may be destroyed, paralyzed, or, in some cases, in contrast, temporarily boosted.

The objective of this chapter is to provide an overview of tillage-based shifts in abundance and diversity and their consequences for interactions between prevailing functional groups. Detailed analysis will be devoted to antagonistic relationships, acknowledging their significance for sustainable agriculture. In restricting the topics of this chapter to meso- and microarthropods (Collembola, Mesostigmatic Acarina, and Diptera) and nematodes, the significance of other soil-inhabiting organisms of soil ecosystems is neither underestimated nor devalued.

10.2 INVERTEBRATES IN SOIL ECOSYSTEMS

Soil is more than an inert medium containing chemical nutrients; it teems with life—the edaphon. Bacteria, fungi, actinomycetes, and algae make up the largest bulk of soil organisms in terms of biomass and diversity. Not only does the functioning of soil ecosystems rely on bacterial processes, but the survival of all other forms of life does as well.⁵ Bacteria occur in almost every environment on the earth and are

involved in the various life processes. Fungi and actinomycetes are vital components of soil formation processes. Microphytes bind mineral soil particles with their threads and the adhesive exudates they release to build stable aggregates; in addition, they are involved in many other functions in soil ecosystems.^{6,7} In terms of biomass, earthworms and enchytraeids rank second within the edaphon, followed by nematodes and gastropods. All the other animals range far behind these groups as a consequence of their lower weight. However, neither the weight nor the taxonomic class of the involved animals can describe their role in soil ecosystems. Animals of the same taxon may accomplish different functions, whereas those of different taxa may participate in the same function. Accordingly, the functional diversity of soil inhabitants differs from the commonly known taxonomic diversity.⁸ As heterotrophic decomposers, soil microbes occupy a key position in nutrient cycling in soil food webs. Ninety to ninety-five percent of all cycling nutrients pass through this group of organisms.⁹ Despite their vital significance, microorganisms cannot sustain the function and stability of soil ecosystems on their own. They essentially depend upon other components to ensure a functioning soil ecosystem. The profound interactions with other cohabitants are too close and too firm to enable system functioning in isolation. Consequently, invertebrates are significant components of soil ecosystems and are responsible for various functions in soil ecosystems. These include:

- Soil building and soil formation
- Amelioration of soil structure
- Supporting soil–gas exchange and water balance
- Nutrient conservation (humus and nutrient pools)
- Dispersal of microorganisms into new niches
- Primary shredding of organic residues (accessibility to microbial attack)
- Contribution to mineralization of organic matter
- Rejuvenation of microbial colonies (refreshing their activities)
- Below ground crop injury (pests and pathogens)
- Regulatory functions as antagonistic agents (predators and parasites)
- Bioindicators for changes in soil environments
- Alternative preys for aboveground predators

All four invertebrate groups addressed in this chapter occur in high numbers, despite their relatively low biomass. Nematodes are the most abundant faunal group in the soil edaphon, followed by Protozoa. Collembola, Acarina, and Diptera rank next but are far behind nematodes. Population assessments of the four invertebrate groups in soils under arable cropping systems with cereal, sugar beet, and field legumes confirmed the highest dominance of nematodes (Figure 10.1).

The numerical dominance of nematodes in soil ecosystems is also found in grassland and forest environments. Dunger¹⁰ reported highest numerical densities of nematodes in grasslands but rather low biomass not exceeding 2.5% of total fauna. Other assessments of nematode fauna in soils under different degrees of human intervention strongly support these observations.^{11–13} Free-living bacterial-feeding nematodes obviously play a key role in decomposition processes and nutrient cycling. The minute body size of nematodes contributes to a higher energy budget per biomass weight unit compared to larger soil animals, leading to efficient turnover rates.

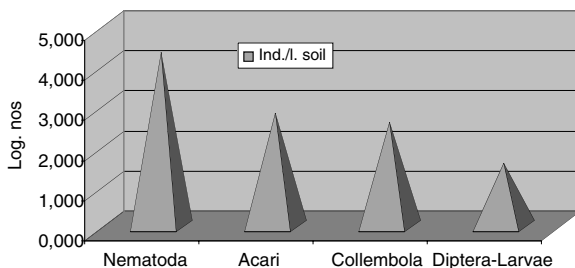


Figure 10.1 The maximum population density (log of individuals/litre soil) of four invertebrate groups in arable soil as monitored between 1983 and 1989 at Lautenbach, Germany.

Nematodes share a number of functions with the mesofaunal arthropods in soil ecosystems. Together with Protozoa, Acarina, Collembola, and Diptera, nematodes present distinct functional groups (guilds) in the nutritional webs of soil ecosystems. Species of the four groups are, for example, parts of the organic-matter-degrading guild in the soil, contributing to decomposition and nutrient recycling. They digest plant assimilates, shed organic residues, and stimulate soil microbial activities. Decaying organic materials provide an essential food source for members of this functional group. Microphytes also may be consumed with the decaying organic matter and consequently serve as alternative food. The specific contribution of a single taxon in a functional group is rather difficult to evaluate *in vivo* due to the close interactions among the organisms. However, the significance of each involved taxon becomes evident when the animal group concerned is excluded. Worldwide exclusion studies based on the litterbag method, soil chemical treatments, or similar techniques^{14,15} provided various indications of the contribution of soil animals in nutrient cycles.^{16,17} Further research inputs are still needed to improve our understanding of the role of animals in soils of agroecosystems.

The few data available highlight the importance of arthropods for mineralization processes^{18–20} reported on arable soils defaunated and reinoculated with collembolan species (*Folsomia quadrioculata* group, *Isotoma notabilis*, *Onychiurus armatus* group, and *Lepidocyrtus cyaneus*.) The presence of the Collembola produced significant effects on nitrogen immobilization ranging between 7 and 9 kg NO₃-N/ha/a.

Apart from the mineralization processes, the four faunal groups under investigation contribute as antagonists to population dynamics of many other cohabitants. Through their predacious or parasitic feeding they may reduce the population density of their prey host species. Within soil food webs predacious species perform population regulatory functions as they feed on microbes and microfauna.^{21,22,163} The inventory of omnivore and fungivore nematodes and arthropods as microphyte antagonists is rather large. As they graze on bacteria or fungi, the prey population declines. The rate of increase of the remaining population rises as a density-dependent response of the prey species, contributing to a dynamic population stability.²³ In the case of mycorrhizae, the stimulated metabolism improves phosphorus (and nitrogen) uptake, promoting metabolism and growth.^{7,24,25,26} Usually abiotic site (microsite) conditions determine the amplitudes of density fluctuations.

Within any soil animal community, burrowing arthropods and earthworms shape the habitats for other soil inhabitants. They also improve gas exchange and water infiltration. Colonization of the new habitats by nonburrowing faunal groups, e.g., nematodes or Collembola, follows when food becomes available. Nematodes are extremely dependent on moisture content in soil pores yet can survive in suboptimal conditions. Predominance of a nematode species ultimately requires a balance between physical, hydrological, and nutritional features of the habitat. This principle applies not only to nematodes but also to all other faunal groups in terrestrial ecosystems.

Soil compaction reduces the proportion of macropores, reducing the available habitat for large soil-inhabiting arthropods. As a consequence, minute (micro) arthropods are likely to dominate in soil animal communities. The body size of the prevailing animals in a soil sample may provide information on soil compaction. The concept of using edaphic species as “bioindicators” is based on the species response to physical, chemical, and biological habitat features.^{27–29,31,94} A large number of species of each of the four taxonomic groups considered in this chapter can function as indicator for soil biological processes. According to Clarholm et al.,²⁷ the abundance of bacteria-feeding nematodes in a nematode community refers to previous bacterial activity, providing more information than assessment of the bacterial populations alone. Close associations between gamasid mites and nematodes^{27–31} or between predatory mites and both nematodes and Collembola^{28,29} have been repeatedly reported to indicate predominance of prey populations in soil. Even the distribution of microarthropods in the rhizosphere is related to the specific feeding pattern of the genera involved. Crossley, Mueller, and Perdue³⁴ reported Astigmatic mites, *Sminthuris*, and Onychiurid Collembola to be closely associated with the root interface, whereas Prostigmatic and Oribatid mites, Onychiurids, and Isotomids Collembola mainly to fungi colonized soil microsites. Karg²² suggested the use of Gamasid mites as bioindicators of soil formation, porosity, or soil compaction.

However, close associations of invertebrates with distinct soil environments may reflect previous conditions rather than a specific feeding pattern. Today there is sufficient evidence that certain Gamasids exhibit a rather high level of feeding preference, e.g., Eviphididae to nematodes, but never reliance on a single nematode species.^{21,35,36} The nematophagous feeding of some mesostigmatic genera may be explained by both habitat sharing on one hand and the some anatomical features of the chelicerae^{28–30,37} on the other. Mites with short dentated cheliceral digits feed primarily, but not only, on nematodes, whereas those with long slender digits and teeth feed on Collembola and other mites.^{28–30,35,37} Despite the observed preferences, both feeding patterns are classified as polyphagous predators.

10.3 ADAPTATIONS OF THE MESOFAUNA TO THE SOIL ENVIRONMENT

Both nematodes and the arthropod groups addressed in this chapter express highly adapted to terrestrial living conditions. This is particularly true for species completing their entire life cycle in the soil. These are the true soil inhabitants, the euedaphic species.³⁸ In contrast, other groups, e.g., several Dipteran genera, only dwell in the

soil temporarily. They remain in soil during the juvenile stages but not as adults. Even though the classification of the edaphon into “eu,” “hemi,” and “ep” edaphic groups^{10,38,39} describes primarily the specific habitat requirements of the animals concerned, it refers roughly to the morphological features of the animals in the different soil strata, pinpointing their degree of adaptation to soil depth. Soil invertebrates show various adaptations to living conditions in soil.

10.3.1 Morphological Adaptations

Specific features of soil invertebrates express the robustness of the taxon involved to live in a given soil environment. As former aquatic animals, Nematoda are rather small (4 mm in length) animals of round and elongated body shape.⁴⁰ The morphology of apertures on the nematode body indicates its affinity to a particular trophic group. Morphology and behavioral features are convincing indicators for soil environments.

Euedaphic Collembola, mainly Onychiuridae and Hypogastruridae, express some similarities with nematodes. Springtails of deeper soil layers are wingless and elongated hexapods, with no eyes. Absence of, or extremely reduced, furcula (the springing organ) is another indication of reduced mobility. In contrast, epigeal or surface-living Collembola, e.g., Entomobiridae, Sminthuridae, are pigmented (UV-protection) with well-developed furcula, strong legs, and eye patches. Similar morphological differences, such as body size, sclerotization, and leg length, found in Collembola also distinguish epigeal from euedaphic mites. Criteria of body size, sclerotization, and leg length used for Collembola also apply to mites. Dipteran larvae share similar morphological adaptations to the other groups in having an elongated body, small size, and no legs.

10.3.1.1 Adaptations to Physicochemical Soil Features

Survival strategies of soil invertebrates reflect their adaptation to the soil environment. Soil type, which presents the geological mineral origin and chemical features, interacts with the edaphon at any given site. Only adapted species thrive in prevailing biotic and abiotic conditions and, consequently, the natural selection pressures. The hypothesis is that soil type may determine abundance and diversity of soil faunal groups. Soil acidity, for example, has been reported to affect some invertebrate taxa. Salmon and Ponge⁴¹ demonstrated in lab experiments that, contrary to field studies, the soil-dwelling Collembola *Heteromurus nitidus* (Entomobryomorpha) can live and even prefers humus with pH < 5.0.⁴² Acidity may be important for soil animal communities at global levels, e.g., climatic zones and regions, rather than within single environments, as it—at least in theory—may exert selection pressure. Differences in species diversity between different habitats, e.g., between forest and arable soils, may be partly due to differing pH effects. Species composition in arable soils seems to be more affected by soil porosity and husbandry effects than by soil pH. Many soil biologists even disagree with the idea that pH may play a role in invertebrate occurrence in arable soils. The coincidence of pH with certain nematode

species may be related to their close association with the host plant species (plant parasitic nematodes) or association to food sources (bacteriovorous/omnivorous) rather than to their innate resistance to acidity. Certain species of plant parasitic nematodes are reported to prevail in environments of a specific pH range.¹¹

Porosity, a further parameter to distinguish soils, has substantial implications for soil water content. Soil moisture is an essential prerequisite for bacteria and fungi, which in turn provide the nutritional basis for various other consumers in soil ecosystems. Unless water, oxygen, and moisture are sufficiently available, soil microorganisms can hardly reproduce and mesofauna can hardly survive. Nematodes, mites, and Collembola are reported to be influenced significantly by soil texture.^{11,43–46} Schmelcher⁴⁶ studied soil fauna in four different soils in undisturbed vineyard environments in Germany. The results obtained are illustrated in [Figure 10.2](#).

Abundance and composition of arthropod populations differed significantly due to soil type. Despite identical climatic conditions, the population of the mesofauna in the calcareous “ranker” was up to one third smaller compared to the corresponding population of the “parabrown” and “pelosol.” Acarina and Collembola prevailed in the parabrown soil, known to provide an optimal ratio between porosity and moisture and consequently favoring microbial activity. Karg²² analyzed associations of mesostigmatic mites to soil types, using worldwide records on Gamasina and Uropodina. His results strongly support the reported associations of soil arthropods with soil type, advocating the use of biological parameters, e.g., microarthropods, for standards to appraise the quality of arable soils.

10.3.1.2 Adaptations to Food Type

A vital factor affecting the distribution of fauna in soil environments is no doubt the accessibility of food sources. Adding organic amendments to agricultural soils or mixing surface residues or excreted feces of animals into topsoils creates centers of microbial activity, interacting with the various species. As in natural ecosystems, the quality of the organic amendment influences nematode populations.⁴⁷ A low C:N ratio revealed adverse effects on phytophagous nematodes. Population responses to organic-matter supply are documented not only for nematodes but also for Collembola, Acarina, and dipterous larvae.^{48,49}

Adaptation of nematode species to food sources is a widely studied subject, particularly in relation to plant parasitic nematodes. The virulence of a nematode species on a host plant cultivar is profoundly determined by the ability of the parasites to overcome defence or resistance mechanisms of the host plant, mainly through specific enzymes. Bacteriovorous and fungivorous feeding patterns of nematodes also indicate adaptation to food quality. Examples are reported on preference of *Aphelenchoides* spp. for some pathogenic fungal species.^{50–52} Predacious nematodes display other enzymatic and anatomical features to overcome prey species resistance.

Like nematodes, mycophagous Collembola show distinct feeding response to available fungus species. Ulber⁵³ identified clear preferences of *Onychiurus fimatus* for some species of soil fungi but avoidance or rejection of others as a main food source, e.g., *Trechoderma* sp. Similar responses were reported for *Folsomia candida*

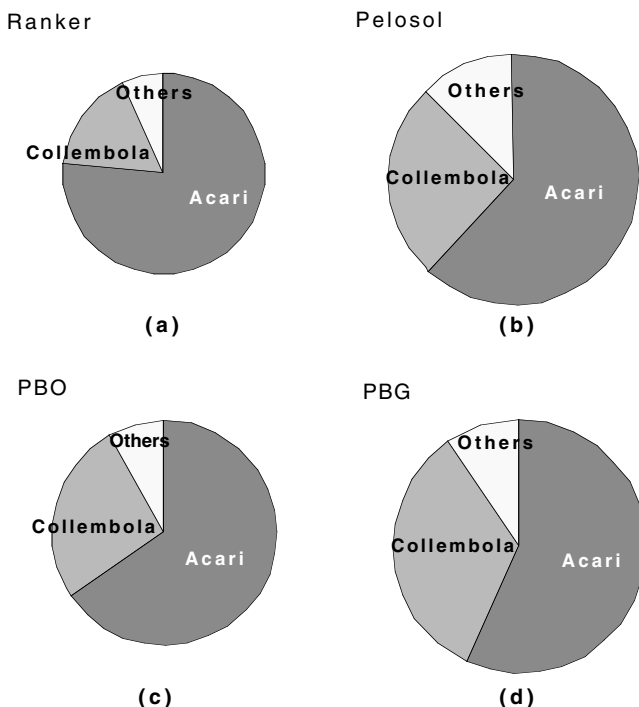


Figure 10.2 The relative population size of soil arthropods in four soil types under viticulture cropping system in Germany. Circle size corresponds to the monitored populations. (a) **Ranker**: soil with sandy loam texture of phyllite origin, described to be, shallow, with low water holding capacity and nutrient contents and at the study site vulnerable for erosion, with pH of 5.34 and organic matter contents of 0.65%. (b) **Pelosol**: made of a calcareous rendzina on a limestone subsoil, clay rich (> 45%) with weak loess silty cover and compacted C-horizon. The microporosity supports a high water-holding capacity, but low water usability. Under dry conditions builds deep fissures, under wet condition poor gas/water permeability. (c) **PBO (Parabrown soil without cover crop)**: a deep rootable (Ah/A1/Bt/Bv/C-Horizontes), soil of sandy loam type, with high water holding capacity, chalk contents of 2% in topsoil, organic-matter content of 0.42% and pH 6.68, and high water available at the study site. (d) **PBG (parabrown soil with cover crop)**. (Data from Schmelcher, 1983. With permission.)

on *Botrytis cinerea*⁵⁴ and *Fusarium oxysporum*.⁵⁵ The available data on mycophagous Collembola justify the assumption that the nutritional adaptation of springtails to their food has evolved. Further investigations are still needed to understand the coevolution principle between the grazer and the fungus species.

As already indicated, habitat features provide the essential framework for associations of mesostigmatic mites and their preferred prey species.¹ The probability of a predator encountering a prey increases drastically when predator and prey share the same habitat. This is obvious for various parasitiformes mites. Nematophagous Gamasids occupy the same soil microsites as nematodes, whereas bacteriovorous Uropodina occur in soil microbial colonies. Unfortunately, information on preferences of terrestrial Diptera larvae for specific food sources is still lacking in

recent literature. Our knowledge of Diptera of agricultural soils in general contains many gaps, despite various contributions.⁴⁹

10.4 MESOFAUNA IN THE EDAPHIC NETWORK

Sustainable populations of soil-inhabiting organisms depend upon a complex network of relationships among the different groups. This network of relationships is commonly well-adjusted and fine-tuned. This is a basic feature of each ecosystem, no matter whether natural or managed, terrestrial or aquatic. The relationships between the organisms can be categorized in three ways:

1. Mutualism
2. Competition
3. Antagonism

Boucher, James, and Keeler⁵⁶ defined mutualism as an interaction between organisms that is beneficial for the participating species. Involved species ought to benefit from one another by their presence or activity, but they are not necessarily in contact with each other. Mutualism is a form of coexistence based on profits for all. In contrast, competition is a situation in which one of the involved species makes better use of the limited resources, whereas the other species is hampered by the reduced resources. Antagonism differs from both mutualism and competition as one species is dependent on the availability of another species⁵⁵ to survive and maintain the population. Antagonism reflects the regulatory potential of an ecosystem. Abundance and species diversity of predators and parasites in a soil roughly reflect the natural regulation potential of the system. Considerable research data are now available from different studies on ecosystem functioning in forest and agricultural soils.^{34,52,57–59}

The special interest in antagonism is mostly related to control of pest species. The integration of natural regulation components into farming is a declared objective of integrated pest management (IPM) and, at the farm scale, integrated farming systems (IFS).^{60–62}

The phenomenon of antagonism is well established in soil ecosystems. Microbial-feeding nematodes, for instance, consume bacterial colonies, fungal mycelia, and spores. In doing so, they contribute to regulation of microphyte populations and, indirectly, to turnover of organic matter, mineralization, and nutrient cycling, as well as to dispersal of bacteria and fungi in soil environments. Evidence of possible interactions between nematodes and soil fungi was obtained from surveys in which fungal spores and mycelia were found to be more abundant in nematode-free soil environments than in soils where nematodes were present.⁶³ This observation was supported by other investigations emphasizing adverse effects on these fungi.⁶⁴ Mycophagous nematodes with a high feeding preference for plant pathogenic fungi are qualified as biological control agents. Roessner and Urland⁵⁰ identified two species of *Aphelenchoides* occurring in high densities on the stem basis of cereal plants being severely infested by the eyespot pathogenic fungus *Pseudocercospora herpotrichoides*. Inoculation of diseased cereal plants with these nematode species on infested cereal plants produced significant reductions in disease incidence under

greenhouse and field conditions. Nagel⁵¹ provided further supporting evidence of these interactions. Hofman, Middelkoop, and Bollen⁶⁵ observed the elimination of *Aphelenchus avenae* by nematicides, which significantly raised the disease incidence of *Rhizoctonia solani* on potato tubers.

Antagonistic nematodes may attack noxious species other than pathogenic fungi. A large inventory of research repeatedly documented appropriateness of *Phasmahabditis*, *Heterorhabditis* spp., *Steinernema* spp., and *Neoaplectana* spp. to control slugs (*Deroceras reticulatum*) and soilborne insect pests.⁶⁶⁻⁶⁸

Like nematodes, various fungus species have been reported as important antagonists of plant parasitic nematodes.⁶⁹⁻⁷⁴ Apart from nematode-trapping fungi,⁷⁵ mostly belonging to the genera *Arthrobotrys*, *Monacrosporium*, *Dactylella*, *Dactylaria*, *Geniculifera*, and *Duddingtonia*, several fungal species are known to parasitize nematode eggs and the sedentary juveniles and females of cyst nematodes.^{69,73,74,76,78} Research reports also refer to *Dilophospora alopecuri* as a fungus antagonistic to seed gall nematodes, *Anguina* spp., known as vectors of bacteria *Clavibacter* (*Rathayibacter*) spp. and the fungus *Dilophospora alopecuri*.

Soil Collembola maintain antagonistic relationships to microphytes, nematodes as well as mites. Studies in forestry, prairie, grassland, and arable soil ecosystems underline the role of Collembola in belowground food webs. Grazing on mycorrhizae, hyphae, and spores of fungi or on bacteria seem to express a graphical reflection of springtail roles in soil ecosystems. They contribute to the dissemination of bacteria and fungal propagules and spores to new microsites⁷⁹ as well as organic matter turnover and acceleration of mineralization processes and nutrient cycles. The predation on soil fungi with obvious preferential feeding behavior is likely to have particular value if the prey fungi are pathogenic to crop plants. Research results obtained under various climatic and cropping conditions,⁸⁰⁻⁸⁴ provided convincing evidence of feeding preference of Collembola to distinct pathogenic fungi. Ulber (1980)⁵³ studied, for example, associations of *Onychiurus fimatus* (Onychiuridae) with both pathogenic and nonpathogenic fungi. The insects showed highest feeding preference for *Phoma betae*, followed by *Fusarium oxysporum*. *Pythium ultimum*, *Aphenomyces cochlioides*, and *Rhizoctonia solani*, respectively, but rejected *Panicillium* spp. and *Trechoderma* spp. Previous observations on *Hypogastrura tulbergi* strongly support these findings.⁸¹ In addition, the arthropods can contribute to dissemination of antagonistic fungi of commercial significance in biological pest control in the soil environment. The collembolan species *Folsomia fimetaria*, *Hypogastrura assimilis*, and *Proisotoma minuta* proved capable of carrying viable conidia of three entomopathogenic fungi (*Beauveria bassiana*, *B. brongniartii* and *Metarhizium anisopliae*), both on the cuticle and in the gut. Although nematodes belong to the diet spectrum of some Collembola,²¹ further research is needed to clarify the feeding selectivity of Collembola with regards to nematodes. This applies notwithstanding the demonstrated remarkable predacious effects of *Tullbergia krausbaueri* and *Onychiurus armatus* on the nematode *T. dubius* *in vitro*.⁸⁵

Soil-dwelling Diptera maintain similar interactions with other soil invertebrates. Dipterous larvae feed on plant debris and may utilize associated microbial flora involved in breakdown and mineralization of organic matter. However, selective feeding tends to be more advanced among these insects compared to other soil

arthropods. Selective feeding on fungi or algae is reported to distinguish distinct dipteran groups.^{86,87} Mycophagous species of Chironomidae feed on soil materials rich in organic matter,⁴⁹ whereas predacious species rely on other soil-inhabiting animals.^{88,89} According to their feeding pattern, dipteran larvae may be separated into five groups⁹⁰—phytosaprophages, surface scrapers, microphages, mycophages, and predators. However, rather little information is available on dipteran relationships with other soil organisms, despite the estimates of their contribution to food webs.⁴⁹

10.5 IMPACTS OF SOIL TILLAGE ON ABUNDANCE AND DIVERSITY

Tillage intervention not only affects the soil environment or soil-inhabiting organisms but greatly influences established relationships between soil organisms as well. Shifts in dominance of species and diversity of communities create remarkable, often long-lasting disturbances. Structural shifts of faunal communities reveal several effects on the functioning of soil ecosystems.⁹² Populations of phytophagous species,⁹³ formerly maintained below economic crop-injury levels, may increase through decline of natural control agents. From this it can be hypothesized that tillage-based disturbances may disrupt the natural balance with the potential to raise new “man-made” pest species. The same principle applies to other components of the soil ecosystem. However, the range of tillage effects on the soil fauna is strongly governed by several other factors, e.g., timing and intensity of tillage, cover crops, manures, and pesticide treatments. Accordingly, responses of the different faunal groups may vary with the taxon under consideration. The most common tillage effects are discussed in the following subsections.

10.5.1 Mesostigmatic Mites

Like many other faunal groups, mesostigmatic mites are influenced primarily by the site features. The population density of these predators varies between 10.000/m² in meadows⁹³ and 17.000/m² in forest.⁹¹ Effects of the soil environment become even more evident when species richness is considered. Like Larink,⁹⁵ Koehler⁹¹ reported rather few species (seven Gamasid species) in sandy soils with low organic-matter content. In contrast, more than 60 species of mesotigmatic mites were found in parabrown soil of higher water and organic-matter content at Lautenbach, Germany.^{45,59}

Gamasid mites are highly dependent on soil pores and burrows as habitats. Pores, burrows, and tubes of decayed roots provide microcorridors or dispersal pathways in the soil matrix.⁹⁶ This underlines the importance of earthworms and enchytraeids for other soil inhabitants. Characteristic habitat specifications, e.g., pore size and moisture, exert a significant effect on the species composition and abundance of Gamasid mites in the soil environment. Karg⁹⁷ even identified specific morphological features of these arthropods that were highly correlated with the specific living conditions in the soil profile. Mites of deeper layers are of minute body size, with reduced leg lengths, and pale or colorless with a more or less flat body shape. In contrast, those living on the soil surface or in the topsoil, e.g., *Parasitidae*, are sclerotized and of

much larger body size, with long legs and high mobility. The distinct morphological characteristics explain the high level of adaptation of mesostigmatic mites to preferred habitats.⁹⁸ However, surveys of Gamasids in other, organic-matter-rich strata⁹¹ showed overlapping characteristics. Despite the small body size of euedaphic species (ranging between 260 and 545 μm , mainly *Rhodacarellus silesiacus*, *Rhodacarus reconditus*, *Dendrolaelaps rectus*, and *Hypoaspis angusta*), a single minute species (e.g., *Lysigamasus misellus*) is classified as a surface-dwelling species. Body dimensions of pure surface dwellers among the Gamasids measure from 650 to 1600 μm . It seems that body size is just one of several components characterizing habitat adaptation. Long-term regular monitoring of Gamasid mite under arable cropping systems revealed supporting argument, as large and pigmented mesostigmatic mite were heat-extracted mainly from topsoil samples, whereas the minute and pale-colored species were found in deep soil layers (Figure 10.3).

The vertical distribution pattern of Gamasids in the soil profile may explain the vulnerability of these arthropods to soil tillage. Former studies in grassland showed that more than 60% of *Rhodacaridae* occurred below 5.1 cm, whereas > 96% of the

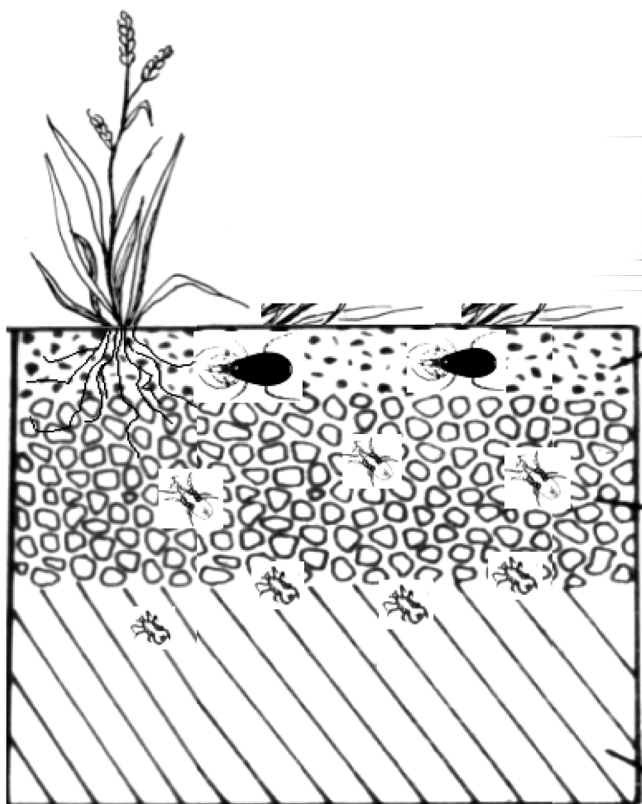


Figure 10.3 Distribution of Gamasid mites in profile of arable soil as extracted from different depths at Lautenbach, Germany between 1980 and 1994, indicating a decline in body size and color from topsoil down to deep soil layers.

Parasitidae colonized the top 0- to 5-cm layer.⁹⁹ The dominance of the minute Rhodacaridae potentially reflected the porosity status at sampling time. Declining soil porosity, e.g., due to compaction, revealed significant shifts in the structure of mesostigmatic communities.^{100–102} Gamasid populations under tractor wheelings declined by 40% on average, with considerable shifts in species composition.¹⁰¹ The greatest response to soil compaction was observed in surface-dwelling *Pergamasus* spp. and in the euedaphic *Rh. silesiacus*.

As a part of soil arthropod fauna mesostigmatic mites are commonly studied in factorial-tillage experiments.¹⁰³ The close interactions between tillage and the various other husbandry components of the farming system, e.g., cover crop, manuring, and disposal of precrop residues, make interpretation of results rather demanding. In addition to annual factorial experiments,¹⁰⁴ tillage effects on mesostigmatic mites were regularly assessed in the context of whole farming systems over 14 years.^{59,105} The system comparison comprised two soil cultivation regimes—noninversion broad-share tine cultivator (Dutzi system) and moldboard plowing, as tillage concepts of integrated farming system (IFS) and conventional farming system (CFS), respectively. Both IFS and CFS were run on six paired field units each (total 36 ha/farming system), IFS following IOBC/WPRS-Guidelines for Integrated Farming⁶⁰ and CFS following regional farming standards. Results of the system comparisons based on two tillage treatments (noninversion tillage and plowing), expressed as annual average density of mesostigmatic mites (arithmetic mean of three sampling occasions/year), are illustrated for two field pairs (Fields I and V) (out of six field pairs under study) in [Figure 10.4](#).

The noninversion tillage of IFS revealed higher mite density compared to CFS plowing. Regardless of crop species, soil type, or annual effects the differences were consistent. In few exceptional cases, there were more mites in CFS soils. The tillage/system effects on mites confirmed previous results on impacts of plowing on these animals.^{45,99,106–109} Some species, e.g., *Rh. agrestis* and *A. siculus*, are reported to be more¹⁰⁹ abundant in plowed soils.⁴⁵ Dunger¹⁰ attributed such effects to the temporarily improved gas exchange after plowing.

10.5.2 Collembola

Collembola exhibit even higher adaptation to terrestrial environments than many acarina. Body shape and size along with morphological characteristics provide reliable information on habitat structure and feeding habits. Dwellers of surface and topsoil are able to resist solar radiation, extreme temperature changes, and flooding. Springing furcula of epedaphic groups reflect the need of these apterogata for open space to disperse. In contrast, inhabitants of deeper soil layers—the euedaphic species—are mostly elongated, pale, and slow-moving animals. Like Gamasid mites, they depend upon the soil pore and burrow matrix as habitat. Their sensitivity to light and high moisture requirements explain why euedaphic species are associated with deeper soil environments.

Numerous research inventories document various tillage effects upon Collembola (and mites).¹¹⁰ Edwards and Loft¹¹¹ reported higher densities of *Hypogastruridae* and *Onychiuridae* in unplowed, paraquat-treated silty clay soils than in conventionally

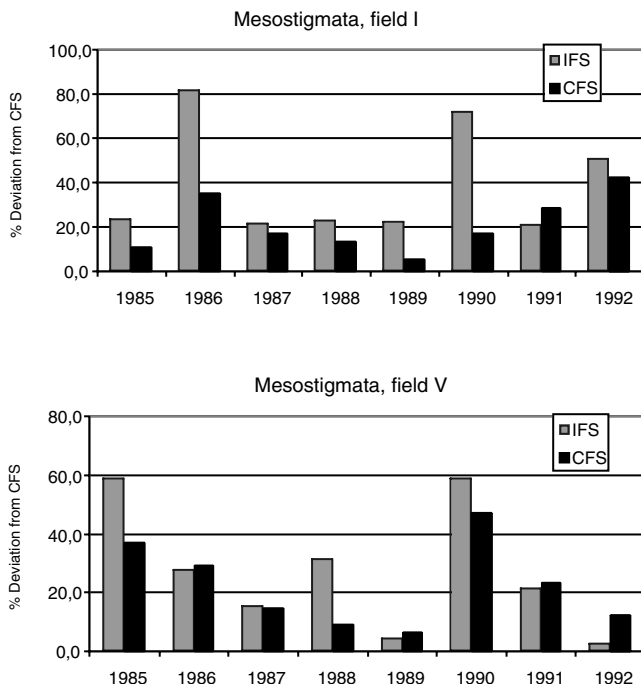


Figure 10.4 The annual density of mesostigmatic mites in tine-cultivated (noninversion [IFS]) and plowed (CFS) arable soils of two field pairs (Field I and V) between 1980 and 1993 at Lautenbach, Germany. (Figures are expressed as arithmetic means of three sampling occasions/year, ten replicates each on six field pairs, with winter, spring cereals, sugar beet, and legumes). (From El Titi, 1999. With permission.)

tilled soils. However, the observed differences in density declined within months. Loring, Snider, and Robertson¹⁰⁶ compared effects of three tillage practices (no-till, moldboard, and chisel) on soil-inhabiting Collembola (and mites) under conditions in the U.K. They found that populations of *Tullbergia granulata* (Onychiuridae/Collembola)—a ubiquitous species of deep-layer communities—declined drastically following tillage. The recovery of the two Collembolan species was similar in both plow and chisel treatments. Significant differences with the no-till treatment were restricted to distinct sampling dates. It was suggested that both mold and chisel-plow tillage stimulate an increase of collembolan (and acarine) populations, presumably due to favorable changes in nutrient availability, pore space, and other physical properties of the soil. Collembola (and Acarina) respond primarily to soil physical features, in particular to soil porosity. Fox et al.¹¹² examined effects of continuous corn grown under no-till and conventional management practices on soil microarthropods near Ottawa, Ontario, Canada. The soil sampling included both traffic and nontraffic rows. Row position had a significant effect on both Onychiuridae and mites (Cryptostigmata and Prostigmata). The researchers attributed the observed differences to variation in the abiotic data.

Matt⁴⁴ compared effects of tine cultivation on Collembola with those of mold-plow in an arable crop rotation in Germany. Due to the 3-year assessments higher population densities of epe-, hemi-, and euedaphic Collembola were found in the no-plow treatment. Results were consistent over the study period. Exceptions occurred, however, in single cases when higher numbers of *Tullbergia denisi* and *T. krausbaueri* were extracted from soil samples taken soon after plowing. The consistent higher abundance of *Onychiurus armatus* in tine-cultivated soils confirmed results of other studies accomplished under several other site conditions.^{10,113,114} Combined effects of tine cultivation and mulch cover on the same onychiurid provided supporting data for the no-plow regime.¹¹⁴ The higher abundance in the noninversion-tillage treatment is attributed to improved nutritional and soil structural factors as well as to seasonal distribution pattern of the Collembola.¹¹³ Long-term effects of two tillage systems (noninversion vs. plowing) as a component of farming systems (IFS and CFS) observed by El Titi⁵⁹ further underlined the reported effects in the other cited studies. Figure 10.5 illustrates results for two of six field pairs at Lautenbach, Germany.

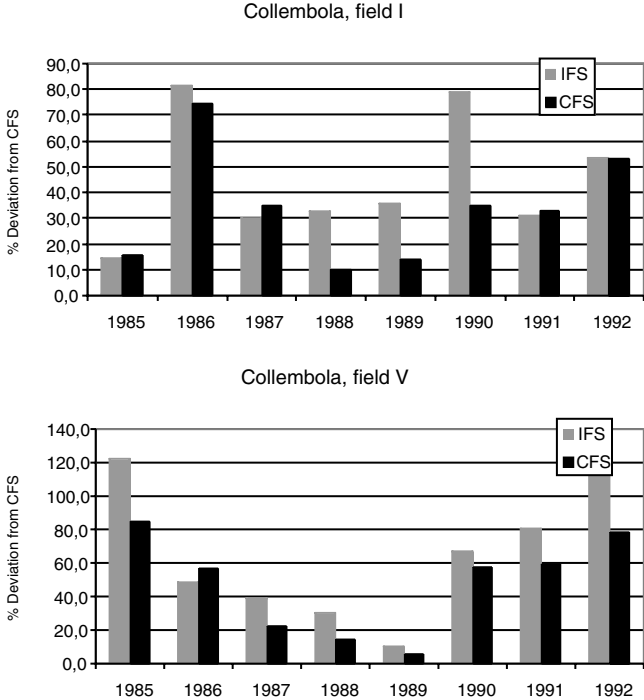


Figure 10.5 Annual average abundance of euedaphic Collembola in tine-cultivated (noninversion [IFS]) and plowed (CFS) arable soils of two field pairs (Field I and V) between 1980 and 1993 at Lautenbach, Germany. (Figures are expressed as arithmetic means of three sampling occasions/year, ten replicates each on six field pairs, with winter, spring cereals, sugar beet, and legumes). (From El Titi, 1999. With permission.)

The observed effects cannot be fully attributed to tillage regimes but are highly affected by the different cultivation interventions. The farming systems used, with their specific differences, are likely to have also contributed to this outcome.

Recovery of Collembolan populations following tillage disturbance seems to be closely related to the life-cycle and dispersal patterns of the prevailing species on the one hand, and availability of food and shelter on the other. Euedaphic species exhibit a more stable population under noninversion tillage compared to the conventional-plowing tillage. In contrast, plowing would reduce populations of surface-dwelling Collembola (mainly Entomobryidae and Sminthuridae) most intensively. Loss of shelter, surface crop, or crop residues as protecting cover or food source and changes of moisture conditions tend to result in a long-lasting decline in epedaphic spring-tails, even after periods for recovery. From soil samples of noninversion-tillage treatments Friebe^{115,116} extracted twice the entomobryids found in soils of the plow treatment at the same site. Sminthurids disappeared completely from the plow treatment but prevailed in tine-cultivation and no-tillage treatments, with the highest density in the latter. As a consequence, a declining disturbance intensity of soil is likely to enhance Collembolan populations. However, other investigations showed that Collembolan communities tended to be more influenced by geographical regions than by the farming regimes.¹¹⁷

10.5.3 Nematodes

Nematodes are the most abundant faunal group among the four invertebrate taxa discussed in this chapter. The food specificity, species diversity, and high abundance of nematodes mean that soil-community studies can be highly informative.^{11,48} Nematode dependence on water films to move and adequate nutritional sources is reflected in their community structure. Therefore, abundance and activity are highly correlated with the prevailing soil biological, chemical, and physical microsite properties. Tillage interventions change these components, with obvious impacts on nematode populations.¹¹⁸ Available research data address tillage effects mostly on plant parasitic nematodes, but increasingly other nematodes of soil food webs are being investigated.^{119–122} Minton¹²⁰ reviewed U.S. research findings on the impacts of conservation tillage (moldboard plow and disk harrow) on nematode populations. Results varied due to species and management but particularly in response to crop residues. Densities of *Meloidogyne incognita* and *Paratrichodorus christiei* did not differ significantly in minimum and conventionally tilled corn plots under monocropping conditions, whereas those of *Scutellonema brachyurum* were highest in minimum-tilled plots only when crop debris was not removed. Alby, Ferris, and Ferris¹²³ found greater population densities of *Pratylenchus scribneri* in conventional-tillage soybean plots than in zero-tillage, due to the higher occurrence of patchiness in conventional fields. Abundance of the soybean cyst nematode *Heterodera glycines* was significantly less in no-tillage plots compared to disked, chiselled, and subsoiled plots but similar to that of plowed plots. Herschman and Bachi¹²⁴ did not find tillage effects on *H. glycines* but in contrast did find effects of wheat residues on the cyst nematode. Planting soybeans in stubble of minimal- or no-tillage treatment may reduce the pest species, apparently specifically.^{125–127} Gavassoni, Tylka, and Munkvold¹²⁷

analyzed the relationships between tillage and spatial patterns of *H. glycines* in two naturally infested locations. Four different tillage systems (conventional tillage, reduced tillage, ridge tillage, and no-tillage) were considered in these investigations. Based on 4 years of data researchers concluded that no-tillage and ridge tillage tended to promote the initially aggregated population of the soybean cyst nematode, whereas conventional- and reduced-tillage systems resulted in a less aggregated spatial pattern.

Villanave et al.¹²⁸ studied the composition of the nematofauna in four soils differing in the length of fallow restoration period since previous cultivation, with the longest fallow period lasting 21 years. One third of the recorded nematode taxa exhibited pronounced responses to cultivation. Mononchidae, Anatonchidae, Tylencholoaimoidea, *Acrobeles*, *Pseudacrobeles*, Tylenchidae, and *Helicotylenchus* preferred sites of more mature successional status, while Dorylaimoidea, *Tylenchorhynchus*, and Rhabdolaimidae dominated the cultivated sites. The maturity index (MI)⁴⁸ did not distinguish between the management regimes. The plant parasite index (PPI) tended to decrease, with higher restoration status linked to greater abundance of the *Tylenchidae* in these situations. The decrease in the ratio of fungal to bacterial feeders in these studies reflected a decreasing importance of the fungal decomposition pathway after resumption of cultivation.

Lack of uniformity in nematode occurrence in soil is likely to be related to the uneven distribution of organic matter in soil environments (hot spots). As part of the participating biota, nematodes cluster to soil organic pockets. Patchiness describes the aggregated distribution pattern of the bacterial and fungal feeders, whereas plant feeders are closely associated with the rhizosphere. Yeates and Bongers⁴⁸ related dissimilarities of nematode communities in forest, grassland, and arable soils to the distinct features of these environments. Bacterial feeding nematode taxa dominated in the forest,^{129,130} which has a distinct, shallow organic layer on the mineral soil, whereas herbivores, omnivores, and fungivores tended to dominate nematode communities of grasslands. Transition from seminatural shrubland through grassland to wheat crop may result in shifts in the ratios of the trophic groups. Yeates and Bird¹³¹ showed that the proportion of plant-feeding nematodes increased from 3 to 51% as conversion took place. Soils with annual crops contain generally fewer nematode species compared to grassland.¹³² Soil texture, moisture, and management were key factors affecting the community structure of nematodes.

Nematodes, in particular free-living plant parasites, show a distinct vertical distribution. Generally, with increasing soil depth, nematode abundance declines. Yeates and Bongers⁴⁸ reported that more than 88% of the total nematode population in a 90-cm profile was found in the top 0–10-cm layer, rapidly decreasing down from 6% in the 10–20-cm layer and to 0.002% in the deepest layer sampled.

Tillage as a major human intervention in soil ecosystems seems to have evident, but not consistent, effects upon nematodes. Freckman and Ettema¹² found that bacterial feeders constituted the greatest nematode populations under annual cropping systems followed by plant feeders, whereas the population of the predacious species was the lowest in grassland, which had the slightest disturbance. Replacing annual plowing by reduced cultivation within a low-input farming approach—IFS—revealed an increase in nematode biomass in a winter wheat–sugar beet–winter

wheat-rotation in the Netherlands.¹³ The greatest response to reduced tillage was found among both omnivores and predacious nematodes. In Germany, Overhoff and Roessner¹³³ compared populations of ectoparasitic nematodes in soil profiles under different tillage treatments (no-tillage, broadshare cultivator [= Dutzi system], tine cultivator, and plow) on the basis of three sampling dates each year. The vertical distribution of nematodes was strongly affected by the tillage regime. Abundance of the four predominant genera (*Merlinius*, *Tylenchorhynchus*, *Helicotylenchus*, and *Paratylenchus*) was lowest under the no-tillage treatment. This was attributed to the extremely low density in the very deep soil layers. In the noninversion cultivation, nematode distribution varied among study sites (three sites), and the difference to plow treatment was inconsistent. Similar effects were observed for migratory nematodes in unplowed soils under continuous wheat cropping.¹³⁴

Disturbances to nematode communities are not restricted to tillage effects only but can be provoked by food sources (e.g., host plant for plant parasitic nematodes, fungi for the mycophagous group), pollutant loads, pH, drought, and management practices. In a 7-year study, Yeates, Wardle, and Watson¹³⁵ monitored nematode communities under an annual (*Zea mays*) and a perennial (*Asparagus officinale*) crop using three weed-management practices (cultivation, herbicide application, and mulching). All management practices influenced the nematode fauna, but the greatest long-term effects came from sawdust mulching. In the mulched plots, there was an initial flush in total and bacterial-feeding species, followed by a decrease reported to coincide with enhanced populations of predacious species. Herbicide did not exert any consistent detrimental effects on nematode communities. The effects of cultivation varied, but under the perennial crop the greatest number of total and bacterial-feeding nematodes was commonly at a depth of 5–10 cm in cultivated plots.

In own studies at Lautenbach/Germany,^{59,136,137} Nematode populations, in particular the plant parasitic groups, were monitored three times a year in both IFS- and CFS-managed soils. During the 10-year study the greatest effect on parasitic species could be attributed to crop species rather than to tillage regime. This was consistent, particularly for cereal (*Heterodera avenae*) and sugar beet (*H. schachtii*) cyst nematodes. Differences in abundance of cereal cyst nematodes in soil and root samples under both tillage regimes showed the effect of the farming system on this noxious species. Results from single field pairs (of six studied fields) is illustrated as an example in [Figure 10.6](#).

The infestation incidence for *H. avenae* was consistently lower in the reduced-tillage treatment of IFS when compared with the conventional plowing system. The observed effect in the long-term assessment matched findings on *H. glycines* in U.S.-based studies as referred to elsewhere. Similar tillage/farming-system effects were also observed for *Ditylenchus dipsaci*,¹³⁷ an endoparasitic plant parasite with a wide host plant and rather high reproductive rate. With the exception of *Pratylenchus* spp., other ectoparasitic nematodes failed to show consistent tillage or management responses in the Lautenbach studies. The initial/final population ratio for *Pratylenchus* spp. (Pf/Pi-ratio) showed a clear management effect and is illustrated in [Figure 10.7](#) for two field pairs (I and II) with differing tillage practices at Lautenbach, Germany.

The pf/pi-ratio of the plow treatment (CFS) was higher than in the tine-cultivated IFS. This is likely to indicate a higher regulation potential for nematodes under

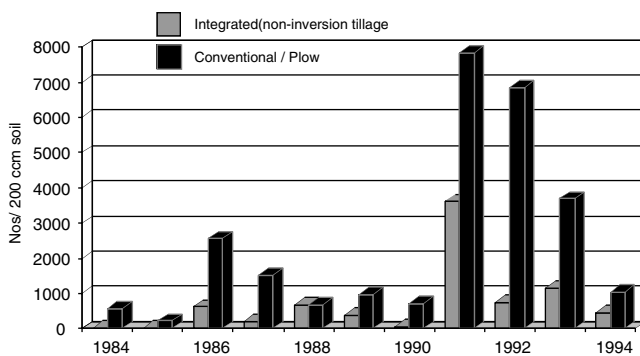


Figure 10.6 Annual average density of the cereal cyst nematode (*Heterodera avenae*)/200 cm³ in soil samples from integrated (= noninversion tillage) and conventional farming systems (plow-tillage) over a 10-year period at Lautenbach, Germany. Figures express the arithmetic means of three sampling occasions/year, in average of six field pairs, three samples of 70 cores each per field, treatment (noninversion vs. plowing), cropped with winter, spring cereals, sugar beet, and legumes). (From El Titi, 1999. With permission.)

IFS soil conditions. The slightly higher abundance of predacious nematodes—Monochidae—in IFS soils (Figure 10.8) is unlikely to be the only factor responsible for the observed lower abundance of *Pratylenchus* spp. Several other mortality factors may be involved.

The high response of nematode communities to disturbance in soil ecosystems is not necessarily restricted to tillage effects alone but may also encompass several other farming-related impact activities. The clarity of their response makes these nematodes a reliable bioindicator for disorder in soil ecosystems. This has been repeatedly proved with regard to crop species to ecotoxicant pollutants,^{138,139} crop residues, and green manuring, as well as in environmental studies.^{11,48,167} However, nematodes should be considered only as one bioindicator component within a bio-indicator assemblage.

10.5.4 Dipteran-Larvae

Most of the research reported on soil-dwelling Diptera has been completed in forestry or grassland ecosystems. The available information on agroecosystems is still limited despite a number of valuable contributions in this field. The abundance of these insects in agricultural soils seems to vary widely. The larval density varies between a few hundred individuals/m² and 8000 (flooded meadow),⁴⁹ ranking far below densities in forestry environments, which average well above 14,000 individuals/m² (see Reference 140). Observed differences are mostly attributed to soil disturbance, organic-matter supply, and soil moisture content. Soil tillage is described as the most detrimental disturbance factor for terrestrial Diptera.^{49,141–143} Higher larval populations were found in no-tillage and minimum-tillage soils compared to soils under plowing. However, exceptions may also occur.⁴⁹ In general, the less soil disturbance,

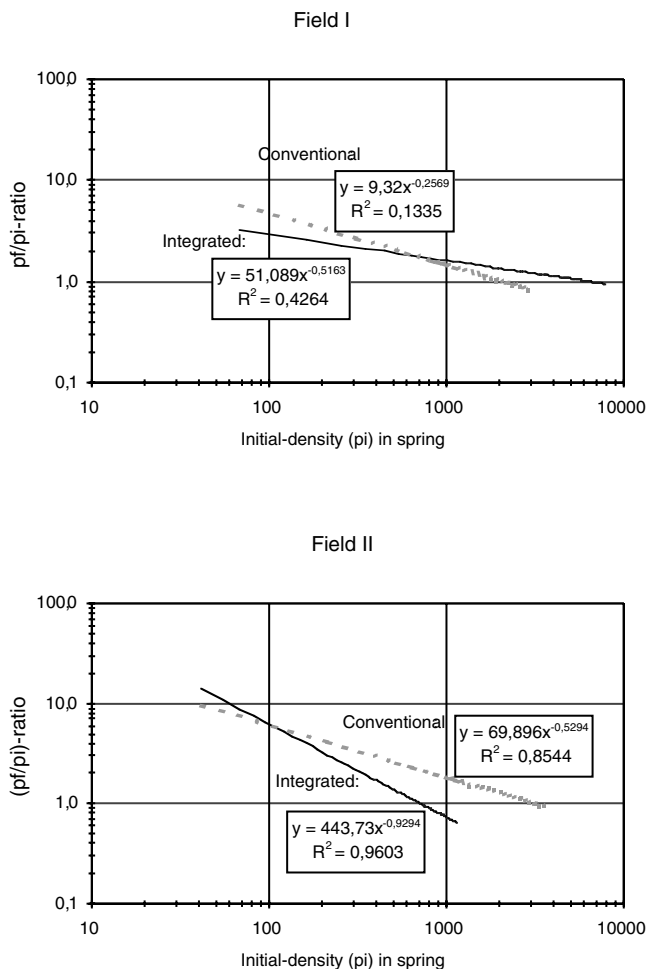


Figure 10.7 The rate of population change—the Pf/Pi-ratio—of *Pratylenchus* spp. under noninversion tillage of integrated and annual plowing of conventional farming systems based on regular monitoring of two fields/tillage treatment, in spring and autumn of each year between 1980 and 1993 at Lautenbach, Germany.

the higher the population density. This explains to a great extent the higher larval biomass under perennial crops, compared to annuals. It is postulated that removal of organic residues from the soil surface by plowing has the most damaging effect, as it takes away an important food source while causing direct damage to larvae and altering habitat structure (mainly porosity and moisture contents).^{49,90}

A comparison of results of larval extraction by flotation with those of adults collected in hatching cages (Photoelectors) shows considerable divergences in the outcome. The larval flotation extraction revealed only ten dipterous families in the 30-cm soil layer, whereas the hatching cages produced 22 families under the same treatment conditions.⁸⁸ This may indicate that there are more dipterous families in

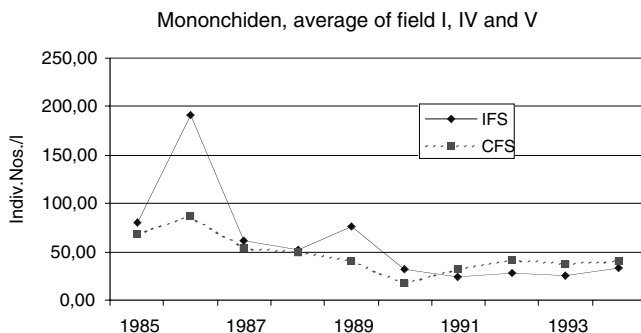


Figure 10.8 The fluctuation in annual density of the predacious nematodes *Monochidae* in tine-tilled and plowed soils as an average of three different fields of the same crop rotation based on monitoring data between 1985 and 1994 at Lautenbach, Germany. (From Heynen and Wuebbeler, 1990. With permission.)

arable soils than the results of extraction suggest. Frouz⁴⁹ reported 50 and 150 spp. for arable systems, indicating a much higher species number of Diptera. The divergence in the results may be attributed to the limited sampling depth in the Lautenbach studies since no soil samples below 0–30 cm were taken. Again, Price and Benham¹⁴⁴ extracted larvae from far greater depths in California than those reported in the Germany studies.

In the Lautenbach studies in Germany,^{59,145} the combined effect of tillage and cover crop on Diptera was addressed using both extraction of larvae from soil samples and monitoring of hatching in cages.^{88,89} When soil physical features were matched, the larval density in the topsoil was higher in the unplowed soil with green manure (IFS) compared to plowed soil without additional organic residues. In contrast, Froese⁸⁹ reported more larvae in the plow treatment in the deeper soil layer (10–30 cm).

Highest larval abundance occurred in topsoil and declined substantially with increasing depth. Unplowed soils of IFS hosted almost no extractable larvae below 20 cm, whereas the highest proportion of the total population assembled in the topsoil. The distribution in the plowed soil, in turn, presented a reversed pattern. Deep soil layers contained the highest numbers, which decreased towards the soil surface.

The observed distribution pattern of Dipteran larvae in arable soils seems to be extremely dependent on the prevailing soil and climatic conditions as well as on the dominant Dipteran families at the site. Nielsen et al.⁸⁷ reported significant reduction in numbers of free-living Cecidomyiidae after tillage, confirming results of other studies on phytophagous species.^{146–148} Data of the Lautenbach comparisons showed differing effects, according to the prevailing families (Table 10.1). The number of cecidomyiid larvae in plowed soil was higher than in tine-cultivated soil.^{88,89}

Adverse tillage effects upon dipteran larvae are often attributed to loss of soil water content.^{149,150} This is particularly true for *Tipulidae*, *Limoniidae*, *Chironomidae*, *Ceratopogonidae*, and *Tabanidae*. Similar effects were observed as green cover, organic-matter supply, or set aside decreased.⁴⁸ Organic amendments, applied as manures or slurry to arable fields or meadows, significantly enhance soil-inhabiting

Table 10.1 Differences in Larval Densities of Diptera in Tine Cultivated (IFS) and Plowed (CFS) Arable Soils in 3-Year Average (1987–1989) with Identical Crop Sequence at Lautenbach, Germany

	IFS (No Plow Tillage)	CFS (Plow)		IFS (No Plow Tillage)	CFS (Plow)
Bibioridae	915	229	Agromyzidae	199	100
Cecidomyiidae	1866	2473	Drosophilidae	172	133
Chironomidae	435	441	Ephedridae	31	26
Sciaridae	2238	2143	Hybotidae	137	175
Trichoceridae	115	411	Phoridae	4938	4569
Empididae	303	256	Dolichopodidae	208	66

See Reference 107 for the data source and the Experimental Design.

Diptera, in particular *Chironomidae*, *Sciaridae*, and *Scatopsidae*.^{156,157} While positive effects of mineral fertilizers on Diptera were observed, they were mostly attributed to improved crop biomass.¹⁴² Other observed responses, for example, to set-aside, herbicides, heavy metal, or drainage were also related to changes in food availability and environmental changes.^{49,152} Long-term effects of tillage regime upon soil-dwelling Diptera can be predicted only when the tillage system practiced is considered in the context of the whole farming system.

10.6 SHIFTS IN RELATIONSHIPS BETWEEN SOIL ORGANISMS

Tillage effects are not restricted to direct impacts on the animal taxa but additionally encompass consequences for the interaction among organisms. Simple interventions may trigger long-lasting effects, disrupting steady-states among organisms. Numerous studies document shifts in antagonistic, mutualistic, and symbiotic relationships. A single treatment of organochlorine insecticide can affect the soil fauna for several years, despite a limited decrease in the total soil population.¹⁵³ Nonsusceptible species often increase, whereas others, in particular predacious species, are much more susceptible. DDT application caused a drastic suppression of predatory mites, leading to an increase in the abundance of prey species, e.g., Collembola.¹⁵⁴ Suppression of Gamasid mites by heavy-metal-loaded manures (sewage sludge) did not induce such suppression.¹⁵⁵ Like pesticides, tillage may induce shifts in system stability. Shifts in the balance between populations appear to be highly dependent on the disturbing factor and the involved species. Described below are a few examples of the known interactions in soil ecosystem of arable crops.

10.6.1 Nematodes/Collembola and Fungal Plant Pathogens

Transmission of pathogens by free-living nematodes to crop plants represents a classical example of the association of nematodes with soil fungi. The literature on fungus-feeding nematodes is increasing rapidly. Much attention is devoted to the genera *Aphelenchoides* and *Aphelenchus*.⁵⁰ *Aphelenchus avenae* has been identified

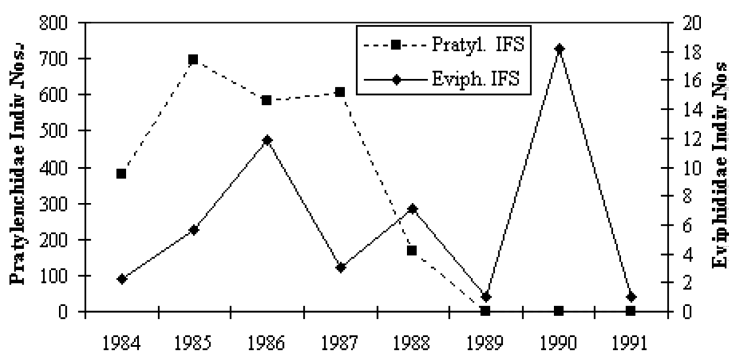
as a species that feeds preferentially on a number of fungal root pathogens, especially on *Rhizoctonia solani* and *Fusarium* spp. Released *Aphelenchoides hematus* successfully reduced the infestation incidence of Eyespot disease caused by the fungal pathogen *Pseudocercospora herpotrichoides*.⁵¹ Feeding on *Verticillium* spp. and *Pythium* spp. by the same nematode trophic group was recorded at other sites.¹¹ The potential of these nematodes for the biological control of plant diseases is still a subject of debate.

The fungivorous soil fauna comprises, in addition to nematodes, a number of Collembola and Acarina.^{157,158} Studies in sugar beet cropping systems provided evidence on the significance of several Collembolan species in controlling soil born pathogens. The collembolan *Onychiurus* s. strongly prefers feeding on *Pythium ultimum*, a pathogen of sugar beet seedling, before shifting to other food sources.^{83,156} Omitting the pathogen, the Collembola, or both from soil under controlled and field conditions documented the significance of the arthropods for crop emergence. Similar observations were reported from U.S. cotton-cropping systems. Releasing of Onychiurids in cotton is reported to significantly reduce the infestation incidence of *Rhizoctonia solani*.⁸⁰ Further studies in the Netherlands showed Collembola to be efficient in controlling *Rhizoctonia solani* on stored potato tubers.¹⁶⁰ Several other investigations confirmed the fungus:collembolan relationship, e.g., for *Mesophorura krausbaueri*, on *Gaeumannomyces graminis* var. *tritici* the fungal pathogen causing take-all disease, and on *Fusarium culmorum* and *Rhizoctonia cerealis* as stem-base pathogens on cereals⁸⁴ and for the collembolan Isotomid *Folsomia fimetaria* against *Rh. solani*.¹⁶¹ Effects of Collembola on Mycorrhizae, a beneficial fungal species, have been repeatedly addressed, acknowledging the function of Collembola¹⁶² but suggesting also that microarthropods may negatively influence the distribution and density of vesicular-arbuscular-mycorrhizae through grazing.

10.6.2 Predatory Mites and Nematodes

Numerous studies have provided evidence of the interactions between predatory mites and nematodes,^{21,28–30,55,85} mostly conducted *in vitro* or in glasshouse environments. Sharma⁸⁵ studied the regulatory effects of *Lasioceius penicilliger* *in vitro*, and both *L. penicilliger* and *Rhodacarus roseus* (Mesostigmata) in potted soil on the population development of predefined populations of *Tylenchorynchus dubius*, Nematoda, a free-living ectoparasite of potato plants. The results revealed a significant predation potential under experimental conditions of over 89%. Karg²⁹ observed negative relationships between potato nematodes and gamasid mite density. However, evidence under open-field conditions is rather difficult to obtain experimentally. Exclusion of single species or trophic group in an undisturbed soil environment is indeed a challenging task in ecosystem field studies. However, data emerging from empirical studies may provide an indication of potential relationships. Regular monitoring of both nematode and mite populations in own studies at Lautenbach, Germany over 10 years, comparing two tillage systems under the same site conditions, revealed some evidence of density-dependent relationships between the free-living nematodes—Pratylenchidae—and the nematophagous Eviphididae (Figure 10.9).

Pratylenchidae - Eviphididae IFS



Pratylenchidae - Eviphididae CFS

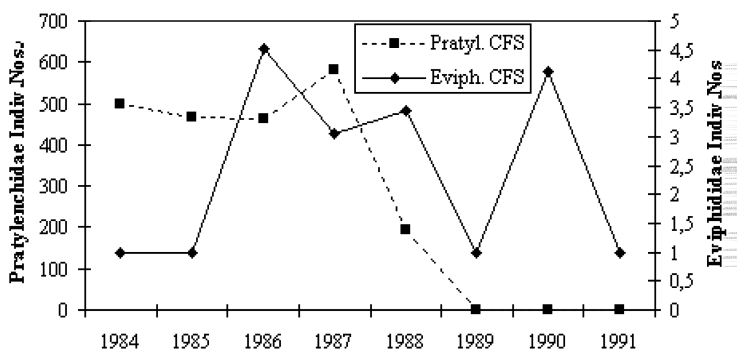


Figure 10.9 The fluctuations of annual population density of free-living nematodes *Pratylenchidae* and the predatory mite *Eviphididae*, in both noninversion (IFS) and plowed (CFS) soil tillage treatments at Lautenbach, Germany. Data are based on three extractions of nematodes and mites at three occasions per year.

The Eviphidid mites tended to produce adverse effects on the nematode. The density of *Paratylenchus* increased as eviphidid density declined. The reciprocal fluctuation of the population densities of both nematodes and mites is likely to underline a predator–prey relationship in this association. However, this indication should not mask other nematode mortality factors in soil ecosystem, e.g., other predatory mites and Nematodes, nematophagous fungi, etc.

There is a long and diverse list of antagonistic interactions between various organisms in soil ecosystems. The cases discussed are just examples to represent the diversity of such interactions and their implication for beneficial control of phytophagous species.

10.7 CONCLUSIONS

Soil invertebrates perform important functions in soil ecosystems, as they contribute to structural improvements, nutrient cycling, and density regulation of soil biota. Understanding of management impacts on these faunal components is an essential condition when aiming for stability of associated agroecosystems. This applies especially to management effects on the complex interactions at the soil-community level. Type and frequency of soil tillage and the associated rearrangement of soil structure are identified as crucial interventions with far-reaching implications for soil nutrient pools¹⁶⁴ and soil organisms. Responses of soil fauna to physical changes in soil environments are rigorously guided by the specific habitat requirements of the species involved. The soil porosity related to a given tillage system is by far the most important habitat feature in soil and consequently restricts faunal inhabitants to pore-size adapted animal species. Dominance of meso- and micropores at a site directly supports meso- and microfauna but hampers large, nonburrowing animals. Similar to structural effects, tillage-related changes in the gaseous and chemical soil phases exhibit selective pressure on faunal communities. With declining tillage intensity community structure becomes increasingly similar to that of grassland and undisturbed environments. A key factor seems to be the tillage-associated alternation in the vertical distribution of crop residues. The proportion of organic residues remaining on the soil surface exerts serious effects on various soil faunal groups, as it severely affects the food webs both above and below the soil surface. Burial of organic residues due to plowing makes food sources for surface living or surface feeding species inaccessible. Lack of food on the soil surface has adverse effects on detritus feeders and their antagonists. Although the range of responses differs widely due to species, site environment, etc., larger organisms in general appear to be more sensitive to tillage operations than smaller organisms. This is particularly obvious for nonburrowing species.

In the subsurface environment, the change in soil gases, water, and temperature resulting from tillage intervention revealed direct effects on microphytes, with subsequent impacts on the associated functional groups. Increasing microbial activity after a tillage event generally lasts as long as the available resources allow. Exhaustion of oxygen in deeper soil environments after a plowing event terminates the aerobic activity of microorganisms. The collapse of aerobic breakdown processes is the expected outcome. Tillage-induced changes in temperature or humidity are likely to strengthen the gas-exchange effects. In contrast, as long as the gaseous exchange continues, oxygen remains available and decomposition processes continue, even if only at lower intensity levels. This is mostly the case under no-tillage and noninversion-tillage approaches. Temporal fluctuations of microbial biomass are commonly followed by responses of correlated faunal groups. Under less-intensive or no-tillage conditions higher system dynamic stability could be expected. Evidence for this correlation has been provided by a number of investigations reviewed as illustrated in this chapter. However, variations in responses found in different studies reflect different magnitudes of tillage disruption and residue burial, timing of tillage operations and measurements, and different soil, crop, and climate combinations.

Investigations of the structure, distribution, and abundance of soil faunal communities have demonstrated three notable points. They are very diverse in numbers of species and highly spatially aggregated and appear to exhibit a low degree of food resource specialization. These observations are most apparent among the nematode and microarthropod assemblages in temperate zones. Bacterivorous and fungivorous nematodes maintain high associations with bacteria and fungi. Their feeding patterns seem to be a part of a comprehensive organizational and functional structure of soil ecosystems. In feeding on nematodes, nematophagous mites (Mesostigmata, Acarina) contribute to density regulation of the microbial populations under given site conditions, supporting stability of the ecosystem. The reported results indicate an extraordinary diversity of soil invertebrates in temperate arable soil ecosystems. Despite remarkable shortfalls in survey and functions of many faunal groups there is a general trend related to tillage impacts. Raising tillage intensity tends to elevate the disturbance in soil ecosystems. Shifts in diversity and abundance occur mostly in combination with shifts in the relationships among the functional groups.

The disturbance level caused by tillage is highly dependent on the associated farming measures. As already mentioned, organic-matter supply is likely to mitigate direct tillage effects on some faunal groups. Other husbandry measures may also intervene to reduce the effects of tillage on the faunal groups addressed in this chapter. The fertilization regimes are reported to have evident effects on nematodes.^{165,166} Porazinska et al.¹⁶⁷ reported nematodes to be affected sporadically by fertilization and irrigation treatments, but mulch had a consistent and frequently significant effect on many herbivores, bacterivores, fungivores, and omnivores. Some species (*Acrobeles*, *Acrobeloides*, *Eucephalobus*, *Teratocephalus*, *Criconemoides*, *Aporcelaimellus*, and *Eudorylaimus*) were always less abundant in mulch-treated plots. However, for various invertebrate groups crop species seemed to have an even greater effect than tillage or other husbandry treatments. In the case of nematodes, there is no consistent pattern governing all trophic groups. Plant parasitic nematodes are highly associated with crop species and may be strongly influenced by crop rotation or even by selection of crop variety. Availability of a resource, such as moisture and food sources, had a much greater effect on nematode abundance than the tillage regime. Some phytophagous species were suppressed under reduced- and no-tillage conditions, whereas others varied in the range of response. Soybean and cereal cyst nematodes were reported to occur in lower densities in unplowed soils compared with plowed. This may contribute to the explanation of the phenomenon of soil suppressiveness, often related to microbial activities.^{167,168} In single studies, populations of *Paratylenchus* spp. were greater in plowed soils. Predatory nematodes (Monochidae) were enhanced during the 5 years following the transition to no-plowing, but the effect did not last longer in the reported study. Phytophagous Diptera also have substantial associations with host plant species. This host alliance strongly underlines the significance of crop rotation for manipulation of populations of noxious species. Phytophagous Diptera showed a much higher larval concentration in topsoil under noninversion tillage and a sharp decline in soil below 10 cm. The distribution pattern of the larvae in plowed soils was reversed after the plowing interventions. Several Diptera showed distinct responses to tillage regime, with

preferences for soil layers, mostly influenced by moisture, organic matter, and other abiotic factors of the soil environment.

Responses of mesostigmatic mites and Collembola are closely correlated to the specific morphology and feeding pattern of the genera. The vertical distribution of gamasid mites is typical, with robust and UV-resistant genera in topsoil or on the soil surface and fine, colorless mites with minute leg lengths at deeper soil layers, and shows the high adaptation to soil layers. Collembola show similar body characteristics that qualify the different species for living at different soil depths. Plowing is found to have the expected hazardous effects on these arthropods, with consequences for the entire soil ecosystem. The adverse effects of plowing seem to intensify when chemical toxicants are applied. The greatest effects were observed when fumigants were used. Similar effects were reported for heavy metal soil contaminations, in particular amendments of heavy-metal-loaded sewage sludge.

In conclusion, the reported studies indicate that reducing tillage intensity to a no-tillage approach would encourage more stability in the soil agroecosystem, enhance diversity, and improve beneficial interactions among soil fauna. An ecosystem-based tillage or no-tillage system can only be one aspect within a comprehensive farming system in which crop rotation, crop cultivar, cover crop, manuring regime, fertilization, and chemical treatments should be tuned and integrated with an IFS.

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